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ENVIRONMENTAL AND TISSUE TEMPERATURES OF SOME TROPICAL INTERTIDAL MARINE ANIMALS

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Intertidal marine animals may be subjected over short periods of time to a broad spectrum of physical conditions. High temperature and desiccation are likely to be important factors for tropical intertidal forms. The importance of these factors has been noted in determining vertical distribution of gastropods, by Broekhuysen (1940). Although they are poikilotherms, it cannot be assumed that the body temperatures of intertidal forms are the same as the meteorological values of the micro-climate which they inhabit. The effects of insolation and evaporation on tissue temperatures of insects and other terrestial arthropods are well known (Gunn, 1942; Parry, 1951; Wigglesworth, 1948; Edney, 1951, and many others). The body temperatures of intertidal marine animals have, however, received little attention, except for a study by Southward (1958) on northern intertidal forms. Southward found body temperatures in many cases to be higher than the local meteorological values, due to retention of sea water and warming by sunlight. In tropical forms one would expect the effect of insolation to be pronounced. The preference of certain intertidal animals for shaded areas has been noted by Lewis (1960) and Broekhuysen (1940).

METHODS

Temperatures were measured with fine wire, copper/constantine, thermocouples insulated with lacquer. The e.m.f. was measured against a reference bath of ice and water in an insulated Thermos flask at 0° C. The recording instrument was a portable potentiometer manufactured by Pye Instruments Ltd., Cambridge, England. An accuracy of ±.25° F. is claimed by the manufacturer. Wet and dry bulb air temperatures were measured with a sling psychrometer.

Three species were selected for study: the barnacle, *Tetraclita squamosa,* the limpet, *Fissurella barbadensis* and the gastropod, *Nerita tesselata.* These species were abundant at the site chosen, a flat platform of beach rock which is fully exposed at low tide. Body temperatures were measured by thrusting the thermocouple tip under the operculum of *Nerita,* through the apical hole of *Fissurella* and between the plates of the carapace of *Tetraclita.* Temperatures of a black body and an inanimate body were also measured. The black body was a piece of soft black mastic and the inanimate body, the shell of a *Nerita,* stuffed with mastic. The deflection of the galvonometer was noted immediately, and each animal was used only for a single temperature measurement.

RESULTS

(a) *Climate of the intertidal zone*

The observed temperatures of the intertidal zone, recorded in Tables I–VIII, clearly indicate that air temperatures measured on the location do not give a complete assessment of the microclimate. The difference between air temperature in a shaded crevice and that of a black body on the rock surface may, for example, be as great as 23° F. on a hot sunny day. On a day with no sun the range of temperatures is not as great. The difference between air shade temperature and black body temperature was only 4° F. on an overcast day.

Throughout the course of observations the temperatures taken in various places measured formed an ascending sequence from wet bulb temperature to black body temperature. The lowest temperatures recorded were those of the wet bulb thermometer, which was cooled by rapid evaporation. The next lowest was the air shade temperature, measured in sheltered crevices close to the water or to a wet rock surface. Dry bulb temperatures were slightly higher than air shade temperatures but lower than air sun temperatures. The differences between these three air temperatures were due to the effects of evaporation and heating

TABLE I

Observations of temperatures in the intertidal zone and of tissue temperatures of barnacles, April 24, 1962, 1200–1300 hours

Air temp. Shade	Air temp. Sun	Dry bulb	Wet bulb	Sea temp.	Rock surf.	Inanim. body	Black body	Tissue temp.
82.2	88.0	87.2	73.0	86.4	95.1	101.0	105.2	94.8
85.3	90.0	86.5	73.5	87.0	95.5	98.8	107.8	101.0
84.3	90.5	86.3	72.3	87.4	95.3	98.8	105.6	99.6
86.4	92.2	86.0	72.5	88.6	95.1	99.6	108.8	97.4
85.3	89.0	86.0	72.7	88.2	95.2	99.2	108.2	99.2
84.3	90.8	85.0	73.5	89.0	94.3	102.8	112.3	102.4
Mean 84.6	90.1	86.2	72.9	87.8	95.1	100.0	107.9	99.1

Weather Remarks: No clouds, bright sun, fresh breeze, low tide 1200 hours.

TABLE II

Observations of temperatures in the intertidal zone and of tissue temperatures of barnacles, May 8, 1962, 1300–1400 hours

Air temp. Shade	Air temp. Sun	Dry bulb	Wet bulb	Sea temp.	Rock surf.	Inanim. body	Black body	Tissue temp.
87.0	87.8	88.0	76.2	94.8	97.4	105.8	110.0	96.8
85.8	88.4	87.5	76.5	95.3	97.2	101.5	110.0	100.8
89.2	91.3	87.5	76.0	94.8	97.2	102.4	111.6	102.0
86.4	90.8	87.0	76.2	96.1	99.2	103.2	109.6	101.0
85.0	91.3	87.0	76.5	95.5	96.4	98.0	106.0	96.8
Mean 86.7	89.9	87.4	76.3	95.3	97.5	102.2	109.4	99.5

Weather Remarks: 5/10 cloud cover, moderate breeze, low tide 1240 hours.

Table III

Observations of temperatures in the intertidal zone and of tissue temperatures of barnacles, July 4, 1962, 1150–1250 hours

Air temp. Shade	Air temp. Sun	Dry bulb	Wet bulb	Sea temp.	Rock surf.	Inanim. body	Black body	Tissue temp.
79.4	79.4	77.3	77.3	83.4	82.0	82.0	83.2	83.8
79.8	79.6	82.6	80.0	83.2	80.5	82.4	86.0	86.4
81.3	80.8	83.3	81.0	83.3	81.8	82.8	87.0	83.8
82.0	82.0	81.2	78.5	83.2	82.0	84.3	87.2	84.0
81.5	82.4	82.0	78.8	83.4	81.5	84.0	87.6	85.0
81.8	82.2	82.0	79.0	83.4	82.0	85.0	87.2	84.3
Mean 81.2	81.4	81.6	79.1	83.5	81.7	83.7	86.6	84.5

Weather Remarks: 10/10 cloud cover after light rain, very light wind, low tide 1000 hours.

Table IV

Observations of temperatures in the intertidal zone and of tissue temperatures of gastropods, May 21, 1962, 1100–1200 hours

Air temp. Shade	Air temp. Sun	Dry bulb	Wet bulb	Sea temp.	Rock surf.	Inanim. body	Black body	Tissue temp.
88.4	93.6	86.5	76.5	93.0	95.2	104.6	111.2	99.0
88.8	89.6	86.0	76.0	93.0	95.1	103.6	111.4	96.1
88.6	88.4	89.0	77.5	93.0	99.8	101.3	105.4	92.4
88.6	93.0	88.0	77.0	93.0	99.6	105.4	112.0	95.5
92.2	91.0	90.1	78.5	93.0	99.2	105.6	114.0	95.5
90.5	91.0	88.5	77.5	93.0	104.4	106.0	116.8	94.0
Mean 89.5	91.1	88.0	77.2	93.0	98.9	104.4	110.1	95.7

Weather Remarks: 2/10 cloud cover, fresh breeze, low tide 1102 hours.

Table V

Observations of temperatures in the intertidal zone and of tissue temperatures of gastropods, July 4, 1962, 1150–1250 hours

Air temp. Shade	Air temp. Sun	Dry bulb	Wet bulb	Sea temp.	Rock surf.	Inanim. body	Black body	Tissue temp.
79.4	79.4	77.3	77.3	83.4	82.0	82.0	83.2	82.2
79.8	79.6	82.6	80.0	83.2	80.5	82.4	86.0	82.2
81.3	80.8	83.3	81.0	83.3	81.8	82.8	87.0	82.4
82.0	82.0	81.2	78.5	83.2	82.0	84.3	87.2	83.6
81.5	82.4	82.0	78.8	83.4	81.5	84.0	87.6	83.6
81.8	82.2	82.0	79.0	83.4	82.0	85.0	87.2	82.0
Mean 81.2	81.4	81.6	79.1	83.5	81.7	83.7	86.6	82.6

Weather Remarks: 10/10 cloud cover after light rain, very light wind, low tide 1000 hours.

TABLE VI

Observations of temperatures in the intertidal zone and of tissue temperatures of gastropods, May 8, 1962, 1300–1400 hours

Air temp. Shade	Air temp. Sun	Dry bulb	Wet bulb	Sea temp.	Rock surf.	Inanim. body	Black body	Tissue temp.
87.0	87.0	88.0	76.2	94.8	97.4	105.8	110.0	85.0
85.8	88.4	87.5	76.5	95.3	97.2	101.5	110.0	86.0
89.2	91.3	87.5	76.0	94.8	97.2	102.4	111.6	85.0
86.4	90.8	87.0	76.2	96.1	99.2	103.2	109.6	82.4
85.0	91.3	87.0	76.5	95.5	96.4	98.0	106.0	82.8
Mean 86.7	89.9	87.4	76.3	95.3	97.5	102.2	109.4	84.2

Weather Remarks: 5/10 cloud cover, moderate breeze, low tide 1240 hours.

TABLE VII

Observations of temperatures in the intertidal zone and of tissue temperatures of limpets, April 10, 1962, 1300–1400 hours

Air temp. Shade	Air temp. Sun	Dry bulb	Wet bulb	Sea temp.	Rock surf.	Inanim. body	Black body	Tissue temp.
83.2	86.0	82.3	72.5	80.0	85.0		96.7	88.8
81.0	84.5	82.3	72.5	80.0	86.0		98.8	86.8
80.5	86.8	82.3	72.5	80.0	85.5		97.5	87.2
Mean 81.6	85.8	82.3	72.5	80.0	85.5		97.6	87.6

Weather Remarks: 8/10 cloud cover (measurements made during sunny periods), strong breeze, low tide 1346 hours.

TABLE VIII

Observations of temperatures in the intertidal zone and of tissue temperatures of limpets, July 4, 1962, 1150–1250 hours

Air temp. Shade	Air temp. Sun	Dry bulb	Wet bulb	Sea temp.	Rock surf.	Inanim. body	Black body	Tissue temp.
79.4	79.4	77.3	77.3	83.4	82.0	82.0	83.2	85.5
79.8	79.6	82.6	80.0	83.2	80.5	82.4	86.0	85.5
81.3	80.8	83.3	81.0	83.3	81.8	82.8	87.0	86.0
82.0	82.0	81.2	78.5	83.2	82.0	84.3	87.2	85.8
81.5	82.4	82.0	78.8	83.4	81.5	84.0	87.6	86.4
81.8	82.2	82.0	79.0	83.4	82.0	85.0	87.2	86.0
Mean 81.2	81.4	81.6	79.1	83.5	81.7	83.7	86.6	85.9

Weather Remarks: 10/10 cloud cover after light rain, very light wind, low tide 1000 hours.

by the sun. Air in shaded crevices received no sunlight and was cooled by evaporation from the water surface. Dry bulb temperatures were taken in the shade, while the air sun temperatures, measured with thermocouples, were not subject to the above cooling influences.

Sea temperatures varied considerably and were observed to be above or below air sun temperature, depending upon the height of the tide. This was due to the fact that measurements were made in tide-pools which, at very low tides, were heated up by the sun and at higher water levels received periodic flushing from the sea. The temperatures of the rock surface were always several degrees above air temperatures, but varied with the degree of wetness.

The two extraneous elements introduced, the inanimate body and the black body, both produced temperatures higher than those measured elsewhere. The black body absorbed the maximum amount of radiation and had invariably the highest observed temperature. The observed temperatures of the inanimate body were lower than the black body but consistently higher than air temperatures. The source of heating above air temperature was presumably mainly the incoming radiation.

(b) *Tissue temperatures*

The results of observations of temperatures relating to the barnacles are shown in Tables I, II and III. Under conditions of full sunlight and a fresh breeze the body temperatures of the barnacles rose 9° F. above that of the air sun temperature. Body temperatures were also 4° F. higher than rock surface temperatures, but below those of the inanimate body and black body of 0.9° and 8.8° F., respectively.

On a partly cloudy day with moderate breeze, tissue temperatures of barnacles were above air sun temperatures by 9.4° and above rock surface temperatures by 2° F. Tissue temperatures were 2.7° lower than inanimate body and 9.9° F. lower than the temperatures of the black body.

Table III contains the observations on a completely overcast day. Temperatures were recorded shortly after a light rain. On this day tissue temperatures were only 3.1° above air sun temperatures and 2.8° F. above the rock surface. The temperatures of the inanimate body were 0.8° lower than tissue temperatures. Black body temperatures were only 2.1° F. higher than tissue temperatures.

On all three days body temperatures of barnacles were above air temperature. The differences were greatest on sunny days and considerably less on an overcast day. It is apparent, then, that the animals absorbed heat from incoming radiation. Body temperatures on sunny days rose nearly as high as the temperature of an inanimate body of the same size and color but not as high as a black body which absorbs the maximum amount of radiation.

The results of observations relating to the gastropod are shown in Tables IV, V and VI. On a day of full sunlight with a fresh breeze, tissue temperatures were 4.6° above the air sun temperature but below those of the rock surface, inanimate body and black body by 3.2°, 8.7° and 14.4° F., respectively.

On a partly cloudy day, body temperatures of the gastropods in shaded crevices were below shade air temperatures by 2.5° and sun air temperatures by 5.7° F. The body temperatures were far below that of an inanimate body by 18° F.

On a cloudy overcast day the difference between tissue temperature and environmental temperature was much less marked. Air sun temperature was 0.6° lower than tissue temperature, and inanimate body and black body temperatures were only 1.1° and 4° F. higher than tissue temperatures.

Thus, on the two sunny days the tissue temperatures of *Nerita* were very close to or below those of the ambient air temperatures. On neither day did they rise as high as the rock surface or inanimate body temperatures. While those specimens in sheltered crevices absorbed little of the incoming radiation, it is apparent that those exposed to the sun do not heat up in spite of radiation absorption.

The results of observations relating to limpets are shown in Tables VII and VIII. On a partly cloudy day, temperatures were recorded during sunny periods. Tissue temperatures were 1.8° above air sun temperatures and 2.1° F. above rock surface temperatures. Black body temperatures were 10° above tissue temperatures.

On an overcast day tissue temperatures were above air sun temperatures, rock surface and inanimate body temperatures by 4.5°, 4.2° and 2.2° F., respectively, but below that of the black body by 0.7° F.

On both days, tissue temperatures were above air temperatures and rock surface temperatures, but below those of the black body. It is apparent that this species is absorbing incoming radiation, but on a sunny day the body heat rises only slightly above air temperature.

Discussion

It is evident from the above results that tissue temperatures of animals living in the intertidal zone are not the same as the ambient air temperatures during exposure. Southward (1958) has attributed the rise in body temperature above sea and air temperatures of intertidal animals at Plymouth to warming by sunlight. Clearly this effect will be much more marked in the tropical forms.

Our results indicate, however, that intertidal animals do not absorb radiation as do inanimate bodies or black bodies. Thus, on a sunny day the tissue temperatures of barnacles are below black body temperatures by 8.8°, the gastropod *Nerita* by 14.1° and limpets by 10° F. Similarly, they were all below the temperature of an inanimate body.

It is thus apparent that there is some factor acting to reduce the heating effect of the sun. The most obvious cooling mechanism is that of evaporation. The effects of evaporation from the cuticle of insects have already been noted. In some insects evaporation may cool the body temperature several degrees C. below the air temperature (Gunn, 1942). It thus seems likely that a similar mechanism may be operative on intertidal animals.

In barnacles the plates of the carapace are tightly closed during exposure. There thus seems little opportunity for evaporation to occur in this species after the initial drying of the external shell. In *Nerita*, however, the foot attached to the substrate remains moist during exposure and the aperture of the shell is never pressed tightly downwards. When a specimen is lifted off the rock, the operculum closes and a drop of water remains in the aperture. This drop feels distinctly cool when placed on the skin. The temperature of the drop measured by a thermocouple did in fact show it to be identical with body temperature of the specimen. In limpets the shell is not firmly pressed against the substrate, so that evaporation can take place around the mantle. Furthermore, in *Fissurella* there is an apical hole through which evaporation can also take place.

In barnacles there is apparently the least opportunity for evaporation to take place, and observed tissue temperatures of this species were closer to those of the

TABLE IX

Water loss in Nerita during exposure on a cloudy day

Spec. no.	Wt. before exposure	Wt. after 1-hr. exposure	Wt. after 2-hr. exposure	Wt. after 4-hr. exposure	Wt. after 6-hr. exposure	Water loss 6 hr.
1.	24.056	24.051	24.046	24.035	24.026	0.030
2.	23.947	23.938	23.930	23.915	23.906	0.041
3.	25.713	25.709	25.703	25.692	25.683	0.030
4.	21.568	21.561	21.557	21.551	21.545	0.023
5.	23.774	23.763	closed			
6.	22.429	22.416		22.398	22.391	0.038
7.	21.507	21.504	21.501	21.493	closed	

inanimate body and black body, than the tissue temperatures of the limpets and gastropods.

Low body temperatures were most striking in the gastropod *Nerita*. In this species the tissue temperatures on a sunny day were lower in relation to environmental temperatures than in the other two species. If evaporative cooling is more effective in this species, then there will be a considerable loss of water during exposure, and hence a loss in body weight. Gowanloch (1926) has demonstrated heavy water loss of northern gastropods during exposure.

The losses in weight of animals exposed in full sunlight and on a cloudy day are shown in Tables IX and X. Each animal was placed on a glass dish with the operculum open and the foot attached to the glass. The glass with animal was weighed to the nearest 0.001 gram before exposure, and again at hourly intervals. Only those animals which kept their opercula open during the exposure period were considered.

The results of Tables IX and X indicate loss of water both in sunlight and on a cloudy day. There is a marked difference in the rate of evaporation, however. On a cloudy day there was a loss of less than 0.05 gm. of water in six hours. On a sunny day the loss in only two hours was between 0.05 and 0.1 gm. It would appear, then, that this species has an effective control over its body temperature by losing water during the exposure period in the intertidal zone through evaporation.

TABLE X

Water loss in Nerita during exposure on a sunny day

Spec. no.	Wt. before exposure	Wt. after 1-hr. exposure	Wt. after 2-hr. exposure	Water loss, 1 hr.	Water loss, 2 hr.
1.	29.161	29.101	closed	0.050	
2.	22.916	22.882	22.863	0.034	0.053
3.	24.167	24.120	24.100	0.047	0.067
4.	23.607	23.540	closed	0.067	
5.	21.554	21.498	21.471	0.056	0.083
6.	20.727	20.703	closed	0.024	

The difference among the three species studied, in resisting increase in body temperatures during exposure, suggests a relation to the vertical distribution of the three forms. At the site chosen, *Fissurella* and *Tetraclita* live at approximately the mid-tide level, while *Nerita,* which has the greatest control over its body temperature, is found at high tide (Lewis, 1960). Thus, the ability of intertidal forms to regulate their body temperatures may, in the tropics, have a bearing on intertidal zonation.

SUMMARY

1. Body temperatures of three common intertidal animals were measured with fine wire thermocouples.

2. Body temperatures were observed to be considerably above ambient air temperatures on a hot sunny day.

3. The difference between body temperatures and ambient air temperatures was less marked on a cloudy day.

4. Evaporative cooling was apparently the mechanism for lowering body temperatures. This process was most effective in the gastropod, *Nerita.*

5. A relationship between ability to regulate body temperature by evaporation and intertidal zonation is suggested.

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